

VARIABILITY AMONG INDIVIDUAL AMERICAN KESTRELS (*FALCO SPARVERIUS*) IN PARTS OF DAY-OLD CHICKS EATEN, PELLET SIZE, AND PELLET EGESTION FREQUENCY

GARY E. DUKE AND AMY L. TEREICK

Department of Veterinary Pathobiology, University of Minnesota, St. Paul, MN 55108 U.S.A.

JAMES K. REYNHOUT

Biology Department, Bethel College, St. Paul, MN 55112 U.S.A.

DAVID M. BIRD

Avian Science and Conservation Centre, McGill University, Ste. Anne de Bellevue, H9X 3V9, Quebec

ALLEN E. PLACE

Center for Marine Biotechnology, University of Maryland, Baltimore, MD 21202 U.S.A.

ABSTRACT.—Seven captive, yearling male American kestrels (*Falco sparverius*) were fed intact 1-d-old chicks (*Gallus domesticus*) (high-fat diet) and eight were fed chicks with yolk sacs removed and replaced with lean turkey meat of equivalent volume (low-fat diet). The number and size of pellets (small, medium, and large) egested per day by each kestrel and the parts of the chicks not eaten were noted; parts and pellets were collected each day for 20 d. One to four pellets were egested per day by each bird. As the number of pellets egested per day increased, their size decreased. There were significant individual variations among kestrels in how often they egested each of the three sizes of pellets; however, diet had no effect on this. Egestion of one ($P = 0.0015$) or two ($P = 0.0023$) pellets per day was most common ($P < 0.05$). There were also significant differences among kestrels in how often they ate chicks entirely ($P = 0$) and how often they ate both legs ($P = 0.0324$), as well as a difference in how often they did not eat the gizzard ($P = 0.0638$) and the entire head ($P = 0.0868$).

KEY WORDS: *Falco sparverius*, pellet egestion, feeding preferences.

Variabilidad entre individuos de *Falco sparverius* en el consumo de partes de pollo, tamaño y frecuencia de producción de egagrópilas

RESUMEN.—Siete machos juveniles de la especie *Falco sparverius* cautivos, comieron pollos (*Gallus domesticus*) intactos de un día de edad y ocho comieron pollos con sacos de yemas removidas y reemplazadas con carne de bajo contenido de grasa y de un volumen equivalente. Se registró el número y tamaño de egagrópilas (pequeño, mediano y grande) producidas por día por cada individuo (*F. sparverius*) y además se tomó nota de las partes de pollo no consumidas (procesadas). Se colectaron partes y egagrópilas durante 20 d. Cada ave produjo de una a cuatro egagrópilas por día. A medida que el número de egagrópilas producidas por día aumentó, su tamaño disminuyó. Hubo una variación individual significativa entre los individuos de *F. sparverius*, en cuanto a cuán a menudo ellos produjeron cada uno de los tres tamaños de egagrópilas, sin embargo, la dieta no tuvo efecto sobre esto. La producción de una ($P = 0.0015$) o dos ($P = 0.0023$) egagrópilas por día fue más común ($P < 0.05$). También hubo diferencias significativas entre individuos en cuán a menudo ellos comían pollos enteros ($P = 0$) y cuán a menudo ellos comían ambas patas ($P = 0.0324$), así como una diferencia en cuán a menudo ellos no comieron la molleja ($P = 0.0638$) y la cabeza entera ($P = 0.0868$).

[Traducción de Ivan Lazo]

The mechanism (Durham 1983) and regulation (Balgooyen 1971, Duke et al. 1976, Fuller et al. 1978) of pellet egestion are fairly well understood in falconiforms. Balgooyen (1971) and Duke et al.

(1976) concluded that falconiforms egest pellets at dawn, whereas strigiforms egest when digestion of a meal is completed (Duke and Rhoades 1977, Fuller and Duke 1978, Duke et al. 1980). While the

food habits and nutritional requirements of falconiforms have been identified for most species, preferences for specific parts of prey have not been adequately described.

The objectives of the present study were to analyze individual variability among American kestrels (*Falco sparverius*) in the number and size of pellets egested per day and the parts of prey that they prefer when on high- and low-fat diets.

METHODS

Fifteen yearling, male kestrels obtained from a captive colony at the Avian Science and Conservation Centre of McGill University and maintained at the University of Minnesota on a diet of laboratory mice for 5 wk (15 September–20 October 1994) while they acclimated to individual cages (38 cm wide, 46 cm high and 46 cm deep), holding room (3.7 m wide, 5.5 m long and 2.5 m high), controlled environment (25–27°C, 45–50% relative humidity and photoperiod from 0700–2000 H), and daily feeding schedule (at 0800 H). Cages were cleaned weekly and fresh water for drinking and bathing was provided daily.

Each bird was fed either an intact 1-d-old white leg-horn chick (*Gallus domesticus*) (high-fat diet) or a chick with the yolk removed and replaced with a piece of lean turkey meat of approximately equivalent volume (low-fat diet). Mean mass of the turkey meat was 10.30 ± 2.65 g (SD) while yolk weights at 21 d of incubation were less, averaging only 2.57 ± 1.53 g (SD). Chicken egg yolks contain 50% neutral fats and 21% phospholipid (Romanoff 1960) so they have far more fat than lean meat. This amounts to an average of 1.82 g of fat per 21-d-old yolk. Lean turkey meat contains about 1.66% fat so the pieces of turkey fed to kestrels contained only about 0.073 g of fat on average. Thus, high-fat fed birds got 26 times more fat than the low-fat fed birds when both groups ate all of the food presented to them.

Kestrels were weighed upon arrival in our laboratory, 2 wk later, and then monthly for the duration of the study. Twenty min prior to each daily feeding, pellets egested during the previous 24 hr period were collected. We recorded the number collected and grouped them into small, medium, and large categories. Pellets were then dried (50°C) for 24 hr and weighed. Uneaten parts of chicks fed on previous days were also collected, identified, and recorded for each kestrel. The number of days each bird ate a particular chick part was recorded and the percentage of the days each part was eaten was calculated. A Categorical Additive Linear Model (Agresti 1990) was then performed to determine individual differences in parts consumed and the number of times particular chick parts were not eaten for low- and high-fat diet kestrels.

For each bird, the number of days that it egested 1, 2, 3, or 4 pellets was recorded. The percentage of those pellets that were small, medium, and large was calculated and the mean percentage was then determined for each kestrel on both the low- and high-fat diets. A Spearman Rank correlation was performed to determine whether a

relationship existed between the size and the number of pellets egested per day.

To determine the average size of pellets egested per day, pellets were given a ranking of 1, 2, or 3, representing small, medium, and large pellets, respectively. The average size of pellets egested by individual birds each day and average pellet size egested by each bird during the entire 20-d trial was determined. A Student's *t*-test was used to compare the average number and size of pellets egested by high- and low-fat fed birds. In order to use the Student's *t*-test, independence was assumed and the Central Limit Theorem was invoked because we calculated the mean of means. This was necessary because we did not independently identify which pellet was egested by which kestrel.

Mean percentage time required for each pellet size on both diets to be egested and the mean percentage time a particular number of pellets was egested each day was calculated for the 20-d collection period. Individual percentages of egestion for each bird and mean percentages were compared using a Categorical Additive Linear Model.

To measure the association between number of pellets egested by kestrels and the parts of the 1-d-old chicks they ate, a Fisher's Exact Test (2-Tail) was performed. All birds were considered together. Unless otherwise noted, all results of all analyses were considered to be significantly different when $P < 0.05$.

RESULTS AND DISCUSSION

Mean body mass of the high-fat fed kestrels was 98.08 ± 3.338 g (SD) at the beginning of the study and 109.62 ± 3.29 g at the end. For the low-fat fed individuals, initial mean body mass was 102.19 ± 2.67 g and final mass averaged 107.21 ± 2.61 g. A repeated measures ANOVA indicated that there was no difference in the effect of diet averaged over all days ($P = 0.7917$) or for each day ($P < 0.3611$) on body mass gain. In comparison with the first day of our experiment, all birds gained mass on each successive day ($P < 0.0005$) but diet had no effect on this ($P < 0.0787$).

Between bird comparisons showed there were significant differences in the percentage of time whole chicks (AW) were eaten ($P = 0$) and when both legs (DeL-2) were not eaten ($P = 0.0324$). There were also differences between birds in not eating the gizzard (DeG) ($P = 0.0638$) and not eating the head (DeH) ($P = 0.0868$) (Tables 1 and 2).

A Spearman Rank correlation analysis indicated no correlation between body mass and the percentage of time kestrels ate prey entirely ($P = 0.09237$). This suggested that individual differences in metabolic rates among kestrels caused some to require less daily food intake than others. Individual preferences may have also been related

Table 1. Percentage of time high-fat fed kestrels ate various parts of 1-d-old chicks over a 20-d collection period.

BIRD	AW ^a	DE-1/2	DEH	DEH-1/2	DEB	DEG	DEL-1	DEL-2	DEY
1	70	0	0	0	5	0	15	15	0
2	70	0	0	0	5	15	15	5	5
3	30	0	5	0	5	0	35	15	15
4	15	0	20	0	10	35	35	15	0
5	25	0	0	0	15	40	20	30	5
6	25	0	5	5	10	30	35	25	0
7	25	10	5	0	10	25	15	25	5

^a AW—ate whole chick; De-1/2—did not eat half of the chick; DeH—did not eat chick head; DeH-1/2—did not eat half of the chick head; DeB—did not eat beak; DeG—did not eat gizzard; DeL-1—did not eat one leg; DeL-2—did not eat both legs; DeY—did not eat yolk.

to differences in metabolic requirements. Eating gizzards ($P = 0.0638$), heads ($P = 0.0868$) or legs ($P = 0.0324$), for instance, probably required more time and effort to reduce these organs to pieces small enough to be swallowed increasing the metabolic needs of kestrels compelled to eat these parts.

To our knowledge, it has not been previously reported that small raptors selectively consume specific parts of their prey. It is known that kestrels select certain kinds of prey (Bryan 1984) or select prey on the basis of size (Marti and Hogue 1979, Overskaug et al. 1995) and activity level (Sarno and Gubanich 1995). Differences in the parts of 1-d-old chicks eaten were not expected because the kestrels used in this study were from a captive-bred colony, all derived over 20 generations from a common genetic stock consisting of 10 pr captured in the Montreal area. Additionally, they were maintained, fed and managed similarly in captivity.

Comparison of low- and high-fat diets revealed that there was no effect of diet on what parts of

the chick the birds did or did not eat ($P > 0.2257$) (Table 3).

A negative correlation between pellet size and the number of pellets egested per day was found for large pellets in both high- ($R = -0.6474$, $P = 0.0008$) and low-fat fed kestrels ($R = -0.7546$, $P = 0.0001$), whereas a positive correlation existed between number of pellets egested and small pellets for both high- ($R = 0.7565$, $P = 0.0001$) and low-fat fed birds ($R = 0.6632$, $P = 0.0003$). The same correlation existed for small ($R = 0.7045$, $P = 0.0001$) and large ($R = -0.6934$, $P = 0.0001$) pellets when all birds were considered together. Thus, as the number of pellets egested per day increased, the percentage of those pellets that were small increased.

Pellets classified as small, medium, or large were weighed and the mean weights for each of the three size groups were determined. On average the small, medium, and large pellets weighed 0.1280 ± 0.0094 ($N = 78$), 0.2541 ± 0.0062 ($N = 178$), and 0.4018 ± 0.0066 ($N = 157$) g, respectively.

Table 2. Percentage of time low-fat fed kestrels ate various parts of 1-d-old chicks over a 20-d collection period.

BIRD	AW ^a	DE-1/2	DEH	DEH-1/2	DEB	DEG	DEL-1	DEL-2	DEM	DEM-1/2
8	20	0	0	0	0	20	0	5	70	0
9	10	5	0	0	5	5	20	40	75	5
10	95	0	0	0	0	0	0	0	5	0
11	10	0	5	0	5	0	10	0	85	0
12	10	0	5	0	5	25	30	10	60	5
13	5	0	30	0	10	0	20	0	80	0
14	10	0	5	0	10	15	25	35	70	0
15	0	0	20	0	10	0	30	30	85	0

^a AW—ate whole chick; De-1/2—did not eat half of the chick; DeH—did not eat chick head; DeH-1/2—did not eat half of chick head; DeB—did not eat beak; DeG—did not eat gizzard; DeL-1—did not eat one leg; DeL-2—did not eat both legs; DeY—did not eat yolk; DeM—did not eat turkey meat; DeM-1/2—did not eat half of the turkey meat.

Table 3. Mean percentage of time (\pm SD) kestrels on high- and low-fat diets ate various parts of 1-d-old chicks over a 20-d period.

PARTS OF CHICK EATEN	HIGH FAT (N = 7)	LOW FAT (N = 8)
AW ^a	37.1 \pm 8.7	20.0 \pm 10.9
De-1/2	1.4 \pm 1.4	0.6 \pm 0.6
DeH	5.0 \pm 2.7	8.1 \pm 3.9
DeH-1/2	0.7 \pm 0.7	0 \pm 0
DeB	8.6 \pm 1.4	5.6 \pm 1.5
DeG	20.7 \pm 6.1	8.1 \pm 3.7
DeL-1	24.3 \pm 3.8	16.9 \pm 4.3
DeL-2	18.6 \pm 3.2	15.0 \pm 6.1

^aAW—ate whole chick; De-1/2—did not eat half of the chick; DeH—did not eat chick head; DeH-1/2—did not eat half of the chick head; DeB—did not eat beak; DeG—did not eat gizzard; DeL-1—did not eat one leg; DeL-2—did not eat both legs; DeY—did not eat yolk.

It is interesting that the kestrels in this study often egested more than one pellet per day when earlier studies (Balgooyen 1971, Duke et al. 1976) indicated that falconiforms egest only one pellet at dawn. This could have been related to the fact that birds in earlier studies were given a meal, then uneaten remains were collected after 1 hr. In our study, food was left for 24 hr so birds had the opportunity to eat several meals and egest several pellets over the day. Digestion of several smaller meals may be more thorough than digestion of one large meal. It is likely that free ranging raptors egest many times daily and, in so doing, their stomachs are not kept partially filled with indigestible materials during the day. This would be especially detrimental to small raptors with high metabolic rates and high demands for daily food intake. Clearly, more studies of pellet egestion should be undertaken using variable feeding times and meal sizes to better simulate natural conditions.

Although there was variability in the number of pellets egested per day among the birds (Table 4), there was not a significant difference in the number of pellets egested per day for the two diets ($P = 0.6994$). High-fat fed birds egested an average of 1.62 ± 0.39 pellets per day, and low-fat fed birds egested an average of 1.55 ± 0.31 pellets per day. There was an effect of diet on the size of the pellets, however, with birds eating the low-fat diet producing significantly larger pellets ($P = 0.0461$). This difference was probably related to the lipid content of the diet. Lipid in the duodenum is

Table 4. Mean number and size (small = 1, medium = 2 and large = 3) of pellets (\pm SD) egested per day by kestrels over a 20-d period.

BIRD	MEAN NUMBER OF PELLETS EGESTED	
	PER DAY	MEAN SIZE OF PELLETS EGESTED PER DAY
1	0.90 \pm 0.79	1.40 \pm 1.18
2	1.80 \pm 0.89	1.77 \pm 0.81
3	1.25 \pm 0.85	1.88 \pm 1.09
4	2.00 \pm 1.08	1.73 \pm 0.66
5	1.80 \pm 0.89	2.05 \pm 0.83
6	1.80 \pm 1.01	1.69 \pm 0.71
7	1.80 \pm 0.83	2.09 \pm 0.48
8	1.85 \pm 0.67	2.07 \pm 0.63
9	1.75 \pm 1.07	1.95 \pm 0.88
10	1.20 \pm 0.41	2.60 \pm 0.50
11	1.00 \pm 0.46	2.35 \pm 0.99
12	1.45 \pm 1.05	1.64 \pm 0.89
13	1.80 \pm 0.77	2.04 \pm 0.63
14	1.70 \pm 0.86	2.20 \pm 0.79
15	1.65 \pm 0.75	1.98 \pm 0.66

known to slow gastric emptying (Duke and Evan-son 1972) and the enterogastric reflex in turkeys and all mammals so far examined (Argenzio 1993). Slowing of this reflex in a raptor on a high-fat diet would increase the time food remains in the stomach increasing gastric digestion and reducing the size of pellets. Since this was the only effect of diet observed, fat content did not appear to be an important factor in overall food intake or digestion in kestrels.

Between bird comparisons showed individual differences in the mean percentage time required for the egestion of small ($P = 0.0417$), medium ($P = 0.0020$), and large ($P = 0.0418$) pellets (Table 5). There was no discernible effect of diet on the percentages for small ($P = 0.3145$), medium ($P = 0.5195$), and large ($P = 0.7516$) pellets. High-fat fed birds egested small pellets 35.7 ± 5.9 , medium pellets 56.4 ± 6.0 , and large pellets $35.7 \pm 5.2\%$ of the time. Whereas low-fat fed birds egested small, medium, and large pellets 26.3 ± 4.9 , 54.4 ± 7.1 , and $44.4 \pm 5.7\%$ of the time, respectively. The total of these percentages is greater than 100% because birds egested more than one pellet a day.

Comparisons of the days kestrels egested 1, 2, 3, or 4 pellets showed significant individual differences in percentages for egesting one ($P = 0.0015$) or two ($P = 0.0023$) pellets per day (Table 6).

Table 5. Percentage of time kestrels egested small, medium, and large pellets over the 20-day collection period.

BIRD	SMALL ^a	MEDIUM ^b	LARGE ^c
1	15	40	20
2	40	70	40
3	35	30	50
4	50	70	20
5	15	70	45
6	55	60	25
7	40	55	50
8	35	65	40
9	45	40	35
10	10	30	70
11	05	25	60
12	35	60	20
13	20	80	40
14	25	65	55
15	35	70	35

^a $P = 0.0417$; ^b $P = 0.0020$; ^c $P = 0.0418$.

NOTE: The total of the percentage for each bird is greater than 100% because each bird may have egested more than one pellet per day.

Comparison of mean percentages showed that diet had no effect on the mean percentage of time high-fat versus low-fat fed kestrels egested zero ($11.4 \pm 26.9\%$ vs. $6.0 \pm 1.9\%$, $P = 0.3554$), one ($35.0 \pm 4.0\%$ vs. $46.9 \pm 3.9\%$, $P = 0.3297$), two ($36.4 \pm 4.1\%$ vs. $35.0 \pm 3.8\%$, $P = 0.2005$), three

Table 6. Percentage of time kestrels egested 0, 1, 2, 3, and 4 pellets per day over a 20-d collection period.

BIRD	0 PEL-LETS ^a	1 PEL-LET ^b	2 PEL-LETS ^c	3 PEL-LETS ^d	4 PEL-LETS ^e
1	35	40	25	0	0
2	10	15	65	5	5
3	15	55	20	10	0
4	5	30	35	20	10
5	10	20	50	20	0
6	5	40	30	20	5
7	0	45	30	25	0
8	0	30	55	15	0
9	5	50	15	25	5
10	0	80	20	0	0
11	10	80	10	0	0
12	15	45	25	10	5
13	5	25	55	15	0
14	10	30	50	5	5
15	5	35	50	10	0

^a $P = 0.3198$; ^b $P = 0.0015$; ^c $P = 0.0023$; ^d $P = 0.4576$; ^e $P = 0.9985$.

($14.3 \pm 3.0\%$ vs. $10.0 \pm 2.4\%$, $P = 0.1081$), and four pellets per day ($2.9 \pm 1.4\%$ vs. $1.9 \pm 0.1\%$, $P = 0.6726$). Zero or four pellets per day were least frequently observed, while one or two egested per day was the most frequent egestion pattern.

A significant association existed between the number of pellets egested and parts of the chick eaten when they did not eat the gizzard (DeG) ($P = 0.014$) and ate only half of the head (DeH-1/2) ($P = 0.023$). It is not clear how not eating the gizzard might affect the number of pellets egested, since the gizzard would presumably be completely digested with no parts incorporated into a pellet. On the other hand, not eating one half of the head could affect the number of pellets egested since parts of the beak and skull may be incorporated into a pellet as would any feathers on the head.

ACKNOWLEDGMENTS

We are very grateful for the advice and assistance of Dr. Vickie King, Statistician, Department of Large Animal Clinical Sciences, College of Veterinary Medicine, University of Minnesota.

LITERATURE CITED

- AGRESTI, A. 1990. Mean response models. John Wiley and Sons, New York, NY U.S.A.
- ARGENZIO, R.A. 1993. Gastrointestinal motility. Pages 336–348 in M.J. Swenson and W.O. Reece [Ed.], Duke's physiology of domestic animals. Cornell University Press, Ithaca, NY U.S.A.
- BALGOOYEN, T.G. 1971. Pellet regurgitation of captive sparrow hawks. *Condor* 73:382–385.
- BRYAN, J.R. 1984. Factors influencing differential predation on house mice (*Mus musculus*) by American kestrels (*Falco sparverius*). *Raptor Res.* 18:143–147.
- DUKE, G.E. AND O.A. EVANSON. 1972. Inhibition of gastric motility by duodenal contents in turkeys. *Poult Sci.* 51:1625–1636.
- , O.A. EVANSON AND A.A. JEGERS. 1976. Meal to pellet intervals in 14 species of captive raptors. *Comp Biochem. Physiol.* 53:1–6.
- AND D.D. RHOADES. 1977. Factors affecting meal to pellet intervals in great horned owls (*Bubo virginianus*). *Comp. Biochem. Physiol. A.* 56:283–286.
- , M.R. FULLER AND B.J. HUBERTY. 1980. The influence of hunger on meal to pellet intervals in barred owls (*Strix varia*). *Comp. Biochem. Physiol. A.* 66:203–207.
- DURHAM, K. 1983. The mechanism and regulation of pellet egestion in the red-tailed hawk (*Buteo jamaicensis*) and related gastrointestinal activity. M.S. thesis, Univ. of Minn. St. Paul, MN U.S.A.
- FULLER, M.R. AND G.E. DUKE. 1978. Regulation of pellet egestion: the effects of multiple feedings on meal to pellet intervals in great horned owls. *Comp. Biochem Physiol. A.* 62:439–444.

- , G.E. DUKE AND D.L. ESKERDHAL. 1978. Regulation of pellet egestion: the influence of feeding time and soundproof conditions on meal to pellet intervals of red-tailed hawks. *Comp. Biochem. Physiol. A.* 62:433–238.
- MARTI, C.D. AND J.G. HOGUE. 1979. Selection of prey by size in screech owls. *Auk* 96:319–327.
- OVERSKAUG, K.E., E. KRISTIENSEN AND P. SUNDE. 1995. Sex-specific diet analysis of the tawny owl. *J. Raptor Res.* 29:137–140.
- ROMANOFF, A.L. 1960. The avian embryo. MacMillan Co Pub., New York, NY U.S.A.
- SARNO, R.J. AND A.A. GUBANICH. 1995. Prey selection by wild American kestrels: the influence of prey size and activity. *J. Raptor Res.* 29:123–126.

Received 7 November 1995; accepted 30 August 1996.